Symmetric replicator dynamics with depletable resources

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The replicator equation is a standard model of evolutionary population game dynamics. In this article, we consider a modification of replicator dynamics, in which playing a particular strategy depletes an associated resource, and the payoff for that strategy is a function of the availability of the resource. Resources are assumed to replenish themselves, given time. Overuse of a resource causes it to crash. If the depletion rate is low enough, most trajectories converge to a stable equilibrium at which all initially present strategies are equally popular. As the depletion rate increases, these fixed points vanish in bifurcations. The phase space is periodic in each of the resource variables, and it is possible for trajectories to whirl around different numbers of times in these variables before converging to the stable equilibrium, resulting in a wide variety of topological types of orbits. Numerical solutions in a low-dimensional case show that in a cross section of the phase space, the topological types are separated by intricately folded separatrices. Once the depletion rate is high enough that the stable equilibrium in the interior of the phase space vanishes, the dynamics immediately become chaotic, without going through a period-doubling cascade; a numerical method reveals horseshoes in a Poincaré map. It appears that the multitude of topological types of orbits present before this final bifurcation generate this chaotic behavior. A periodic orbit of saddle type can be found using the symmetries of the dynamics, and its stable and unstable manifolds may generate a homoclinic tangle.

In the field of evolutionary game dynamics, a standard mathematical model is the replicator equation, which represents the behavior of an infinite population of individuals playing an abstract two-player game. A strategy that earns a higher payoff than the populationwide average will become more common, at the expense of strategies with lower payoffs, representing evolution by selection. If game payoffs are constant, the dynamics are well understood. In this article, we consider a modification in which the payoff for playing a strategy is not constant, but is a function of how much of an abstract resource is available. Playing a strategy consumes some of the associated resource. Each resource replenishes itself naturally. If a resource is depleted so rapidly that the available amount drops below a tipping point, it will crash and the associated strategy will become very expensive until the resource has time to recover. To keep the model tractable, we focus on a highly symmetric case. The resulting model has surprisingly complex behavior. A parameter controls the overall rate at which resources are depleted. For small values of this parameter, the population generally settles at a stable equilibrium, with some resources experiencing crashes beforehand. When it exceeds a threshold, the stable equilibrium no longer exists. Resources crash as soon as they are renewed, resulting in chaotic oscillations.

I. INTRODUCTION

The replicator equation represents natural selection acting on a population in which several strategies for playing an abstract game compete. In the original formulation, the fitness associated with playing a particular strategy depends on a constant payoff matrix and the population state, that is, the fraction of the population that currently uses each available strategy. The dynamics in this case are well understood¹¹. It is typical for populations to converge to an evolutionarily stable state if one exists, for example. In this article, we formulate a novel modification to the standard replicator equation in which each strategy is associated with a resource, and the resource is consumed in proportion to the popularity of the strategy. In isolation, each resource is governed by dynamics similar to an excitable unit from theoretical neuroscience, with a rest state at its maximum level. After a small perturbation, the resource quickly returns to its rest state. Perturbing it past a tipping point causes it to crash to its minimum level, then recover over time to its rest state. Continuous depletion of the resource at a low rate causes it to settle at an equilibrium close

to its maximum, but if it is depleted too rapidly, the equilibrium vanishes in a bifurcation, and the resource experiences continual crashes. When several such resources are coupled to replicator dynamics, the combined behavior is remarkably complicated.

In this article, only the most symmetric case is considered. The strategies are interchangeable and the dynamics are invariant under parallel permutation of population state variables and resource variables. It is therefore possible to identify and analyze all fixed points and bifurcations of the dynamics for an arbitrary number of strategies¹³. A parameter β controls the overall time scale of resource consumption. For low values of β , most trajectories converge to a stable fixed point, in which all strategies are equally popular. For larger values of β , that fixed point vanishes in a degenerate saddle-node bifurcation, and it appears that there are no longer any stable orbits. The result is an immediate transition to chaos, with no period-doubling cascade.

In Section IA, essential background on the standard replicator equation is given. A differential equation for the type of resource under consideration is formulated in Section IB. It is not derived from any specific application. It is meant as a general, simple representation of a renewable resource that cannot be permanently exhausted. Combined replicator-resource dynamics are formulated in Section IC.

A sink and a source in the interior of the phase space are described in Sections II A and II B. These steer the behavior of most trajectories in the interior of the phase space. For the case of two strategies, fixed points on the boundary of the phase space are found and analyzed in Sections II C and II D. Generalizing to any number of strategies, fixed points on the boundary are found inductively, based on the number of strategies that are permanently extinct on various parts of the boundary. This process is given in Section II E.

Bifurcations are found in terms of the depletion rate parameter β . As β increases, the first bifurcations are of saddle-node type, in which some fixed points on the boundary collide and vanish. Once this happens, trajectories are able to whirl around the interior of the phase space in complicated ways, the details of which are given in Section II F. This whirling represents resources experiencing a finite number of crash-and-recovery cycles before the population reaches a stable equilibrium.

The last bifurcation is the collision of the two interior fixed points, described in Section II G. Once this happens, there appear to be no stable orbits left in the phase space, and the dynamics immediately become chaotic. Numerical evidence of horseshoes in a Poincaré map supports the claim that the irregular oscillations are indeed chaotic. The symmetry of the dynamics forces a certain periodic orbit of saddle type to exist in this regime, as explained in Section II H. Its stable manifold may be important in organizing the chaotic trajectories.

These results for the relatively simple, highly symmetric case of replicator dynamics with depletable resources open the path to considering more complicated dynamical systems. In Section III, conclusions are drawn and further topics of investigation are proposed.

A. Background on replicator dynamics

The basic replicator equation is formulated as follows¹¹. Consider a population of individual organisms, each of which is of some type $k \in \{1, 2, ..., K\}$. The number of types K is finite. The population is well mixed and unstructured, so that individuals interact with each other uniformly. In contrast to the discrete Moran and Wright-Fisher models^{4,18}, it is assumed that the number of individuals is large enough that an infinite population approximation with continuous time is appropriate. That is, rather than keep track of the number of individuals of each type, the population state is represented by variables $x_1, x_2, ..., x_K$, where each x_k is the fraction of the population of type k. Thus, the population is represented by a time-dependent state vector $\mathbf{x} = (x_1, x_2, ..., x_K)$ that takes values in a K-vertex simplex \mathscr{S}^K ,

$$\mathscr{S}^{K} = \left\{ \left(x_{1}, x_{2}, \dots, x_{K} \right) \middle| 0 \le x_{k}, \sum_{k} x_{k} = 1 \right\}.$$

$$(1)$$

Reproduction is asexual and without mutation. Associated to each type k is a real-valued fitness c_k that is a function of the environment, including the population state. The rate of change of x_k is jointly proportional to x_k and to the difference between the fitness c_k and the average fitness ϕ ,

$$\phi = \sum_{k} x_k c_k, \text{ or in vector notation, } \phi = \mathbf{x} \cdot \mathbf{c}.$$
 (2)

This results in the general replicator equation,

$$\dot{x}_k = x_k(c_k - \phi) \tag{3}$$

where the dot indicates the derivative with respect to time *t*.

It is typically assumed that each type corresponds to a strategy in an abstract two-player game, and it is in this context that Eq. (3) was originally formulated^{19,20,22}. The game is specified by a payoff matrix **A**, in which the entry $A_{k,j}$ is the payoff earned by a player of strategy k when interacting with a player of strategy j. The game is symmetric in the sense that all players have the same inventory of strategies. The fitness of type k is the expected payoff for playing strategy k when the opposing strategy is distributed according to the population vector,

$$c_k = \sum_j A_{k,j} x_j$$
, or in vector notation, $\mathbf{c} = \mathbf{A}\mathbf{x}$, (4)

as if every member of the population is continuously playing every other member. Given these assumptions, the dynamical system Eq. (3) may be derived as a change of variables from generalized Lotka-Volterra dynamics¹¹.

The dynamical system Eq. (3) has several important properties. It is expressed with *K* variables x_k , but the constraint $\sum_k x_k = 1$ reduces the number of degrees of freedom by 1. The phase space in Eq. (1) is part of a hyperplane \mathcal{H} of dimension K - 1 in \mathbb{R}^K ,

$$\mathcal{H} = \left\{ \left(x_1, x_2, \dots, x_K \right) \middle| \sum_k x_k = 1 \right\}$$

= { **x** | **x** · **1** = 1 } (5)

where **1** is the vector of all 1s,

$$1 = (1, \dots, 1).$$
 (6)

Consequently, one of two methods must be used when studying the dynamics of Eq. (3). The first will be called the *reduced system method*, which is to eliminate the variable x_K , and replace it with $x_K = 1 - x_1 - x_2 - \cdots - x_{K-1}$ in the remaining equations. That substitution leaves K - 1 differential equations in K - 1 variables, which matches the number of degrees of freedom, but the resulting differential equations are more complicated.

The second will be called the *extended phase space method*, which is to think of **x** as an element of \mathbb{R}^K and treat \mathscr{S}^K as an invariant manifold and trapping region within \mathbb{R}^K . This method preserves the simplicity of the differential equations, but requires the consideration of system states **x** that are not in \mathscr{S}^K and are therefore not interpretable as population states.

To confirm that the hyperplane \mathscr{H} is invariant under Eq. (3), define

$$M = \sum_{k} x_k \tag{7}$$

and observe that

$$\begin{split} \dot{M} &= \sum_{k} \dot{x}_{k} \\ &= \sum_{k} x_{k} \left(c_{k} - \phi \right) \\ &= \left(\sum_{k} x_{k} c_{k} \right) - \left(\sum_{k} x_{k} \right) \phi \\ &= (1 - M) \phi. \end{split}$$

Therefore, if any point on a trajectory satisfies M = 1, then the entire trajectory does as well, so it lies within \mathcal{H} .

The boundary of \mathscr{S}^K consists of lower-dimensional simplices formed by points **x** where some of the coordinates are 0. Conceptually, each such face consists of population states where one or more types is permanently extinct. Each face is invariant under Eq. (3), because if any point on a trajectory satisfies $x_k = 0$, then $x_k = 0$ for all time. If a type is extinct at some time, there is no mechanism in the dynamics to cause it to appear at a non-zero level. In particular, mutation is not part of the basic replicator dynamics under consideration here. The faces of \mathscr{S}^K are barriers to the dynamics, because if a trajectory were to cross through one, it would violate the uniqueness of the solution to the initial value problem at that point. Thus, extinction in finite time is not possible in replicator dynamics. If a type is present in the population at a non-zero level at any time, it is permanently present, although it is possible for x_k to converge to 0 as $t \to \pm\infty$. Since \mathscr{S}^K lies within the invariant hyperplane \mathscr{H} and its entire boundary acts as a barrier under the dynamics, the whole simplex is invariant under the dynamics.

Given a set $L \subset \{1, ..., K\}$ of type indices, one can consider the dynamics of Eq. (3) supposing that all types outside of *L* are extinct. That means x_k is permanently 0 if $k \notin L$, and the collection of x_k for $k \in L$ is effectively a lower-dimensional instance of replicator dynamics. This nested structure is useful in understanding the dynamics, as results that hold for a general number of types can be applied to the phase space as a whole and to each of the boundary simplices.

Many variations on Eq. (3) are possible. For example, the dynamics may be modified to include mutation and learning, in which case chaotic dynamics are possible^{13–16}. One can also introduce multi-player games²⁴ and spatial structure³. It is possible to formulate similar dynamics as an iterated map in discrete time, and these can have very complex behavior¹⁷.

Generally, it is assumed that the payoff matrix A is constant, in which case a great deal is known about Eq. (3)¹¹. However, a constant A implies a constant environment, in contrast to nat-

ural environments, which fluctuate. The new feature considered in this article is to suppose that fitness depends on depletable resources in the environment, which means that a constant **A** is no longer sufficient. Once **A** is allowed to vary, the possible behaviors of Eq. (3), or most other population game dynamics, become almost unlimited, and complete mathematical analysis is no longer possible. Some restrictions must be placed on the dynamic environment. For example, one could consider seasonal variation⁸; augmenting a game matrix when a mutant appears¹²; or modeling the environment as a Markov chain¹. For this article, the restrictions are that coupling between resources and strategies is one to one, that the fitness of strategy *k* depends only on the associated resource, and that resources follow identical dynamics derived from the basic model developed in Section **IB**. The resulting system of differential equations is invariant under permutations of the indices, and this invariance facilitates the analysis.

B. Formulation of resource dynamics

In this section, the dynamics of a general renewable resource variable θ are developed. The phase space of θ is generally taken to be the circle \mathscr{T}^1 . The notation $\theta \cong \ldots$ will be used to mean that $\theta \in \mathscr{T}^1$ can be thought of as the given real number plus an unspecified integer multiple of 2π . An = will be used in a few cases where it is helpful to use \mathbb{R} as the phase space because the magnitude of θ as a real number is relevant. In the absence of depletion, the dynamics for θ are

$$\dot{\theta} = \cos\left(\theta + \gamma\right) - \cos\gamma.$$
 (8)

The real number $\gamma \in (0, \pi/2)$ is a constant parameter that controls the locations of two equilibrium states. The restriction on γ is so that $0 < \sin \gamma < 1$ and $0 < \cos \gamma < 1$. By design, under Eq. (8), θ has a stable equilibrium at 0 and an unstable equilibrium at -2γ , as in Fig. 1. Direct substitution confirms that $\dot{\theta} = 0$ at these two numbers, and linear stability analysis confirms that they have the intended stability.

The equilibrium at $\theta \cong 0$ represents the state of maximum availability of the resource. The equilibrium at $\theta \cong -2\gamma$ is a tipping point. If θ is perturbed past -2γ , the dynamics take it the long way around the circle before it returns to 0, which represents a crash in the resource followed by recovery. Such an excursion is roughly analogous to an action potential followed by a refractory period in an excitable neuron⁶. The dynamics in Eq. (8) are essentially the same as the Ermentrout-Kopell canonical model of an excitable unit^{5,7}.



Figure 1. Phase portrait of Eq. (8). The green dot is the stable equilibrium at $\theta \cong 0$, and the red dot is the stable equilibrium at $\theta \cong -2\gamma$. For this picture, $\gamma = \pi/4$.



Figure 2. Phase portrait of Eq. (9). The green dot is the stable equilibrium at $\theta \cong \overline{\theta}_+$, and the red dot is the stable equilibrium at $\theta \cong \overline{\theta}_-$. As *d* increases, the equilibrium points move closer together as in (b). In (c), $d = 1 - \cos \gamma$ and they collide at the blue dot. In (d), $d > 1 - \cos \gamma$ and they no longer exist.

To incorporate depletion of the resource at a constant rate d > 0, an extra term is inserted into Eq. (8) yielding

$$\hat{\theta} = \cos\left(\theta + \gamma\right) - \cos\gamma - d. \tag{9}$$

For small values of d, there are still two equilibrium points located at

$$\bar{\theta}_{\pm} = -\gamma \pm \arccos(d + \cos \gamma).$$

Linear stability analysis confirms that θ_+ is stable and θ_- is unstable. As *d* increases, the equilibrium points move closer together. When $d = 1 - \cos \gamma$, they collide, and for larger *d*, they do not exist. This is a standard saddle-node bifurcation, as shown in Fig. 2. After the bifurcation, θ whirls irregularly without stopping. Conceptually, $d > 1 - \cos \gamma$ means that the depletion rate *d* is so high that the resource repeatedly crashes and recovers.

In Section IC, the fitness derived from using the resource is $\cos \theta$, which is maximized at $\theta \cong 0$. Thus, when the resource is depleted at a low rate and the population approaches a stable equilibrium, θ will converge to a steady state at which the fitness is less than the maximum, representing the fact that when a non-zero portion of the population uses the resource, the payoff from playing the corresponding strategy is reduced by some implicit cost of the resource that increases with the demand.

Other resource dynamics could be considered, of course. The differential equation given in Eq. (9) was chosen because it is relatively simple, requires only one dynamic variable, does not allow the resource to be permanently exhausted, settles at an equilibrium of sub-maximum fitness when depleted slowly, and results in interesting combined replicator-resource dynamics.

C. Formulation of combined replicator-resource dynamics

The remainder of this article is concerned with the dynamical system defined in Eqs. (10) to (11) as follows.

Assume that there are *K* strategies in an abstract game, each of which requires the consumption of a single resource. The payoff for playing strategy *k* is $c_k = \cos \theta_k$, independent of the population state. Combining this payoff with Eq. (3) yields

$$\dot{x}_k = x_k \left(\cos \theta_k - \phi\right) \tag{10}$$

where ϕ is as in Eq. (2),

$$\phi = \sum_k x_k \cos \theta_k.$$

The resource variables θ_k change according to a modification of Eq. (9),

$$\dot{\theta}_k = a \times (\cos\left(\theta_k + \gamma\right) - \cos\gamma - \beta x_k) \tag{11}$$

where a > 0, $0 < \gamma < \pi/2$, and $\beta \ge 0$ are parameters. The dynamics are clearly symmetric under parallel permutations of the x_k 's and θ_k 's.

The time variable *t* is scaled so that one time unit corresponds to approximately the natural lifespan of the species. The overall factor *a* in Eq. (10) determines the timescale of resource depletion compared to the timescale of birth and death. If a > 1, then depletion is rapid enough to significantly affect an individual during its lifetime. If $a \ll 1$, then depletion is slow, and several generations must pass before its effects are felt.

The parameter β , which controls the rate at which the resource is consumed relative to its natural dynamics, is particularly important. The βx_k term in Eq. (11) is the scaled rate at which resource *k* is depleted, and corresponds to *d* in Eq. (9). For small βx_k , depletion amounts to a small perturbation of θ_k that pulls it just a bit away from 0. Since $0 \le x_k \le 1$, this behavior is inevitable when $\beta \ll 1$. If β is large enough and $x_k \approx 1$, depletion pulls θ_k past the tipping point and sends it on an excursion, representing the crash and recovery of resource *k*.

The phase space can be thought of as a *K*-vertex simplex \mathscr{S}^K crossed with a *K*-dimensional torus \mathscr{T}^K ,

$$\mathscr{X}^{K} = \mathscr{S}^{K} \times \mathscr{T}^{K}$$
$$= \left\{ \left(x_{1}, \dots, x_{K}, \theta_{1}, \dots, \theta_{K} \right) \middle| 0 \le x_{k}, \sum_{k} x_{k} = 1, \theta_{k} \in \mathscr{T}^{1} \right\}$$

The notation $(\mathbf{x} | \boldsymbol{\theta})$ will be used to mean the concatenation of a population state vector \mathbf{x} and a resource state vector $\boldsymbol{\theta}$ into a single long vector, as in $(x_1, \ldots, x_k, \theta_1, \ldots, \theta_K)$. The interior of \mathscr{X}^K is all points $(\mathbf{x} | \boldsymbol{\theta})$ for which no x_k is zero. The topological boundary $\partial \mathscr{X}^K$ is an invariant manifold consisting of those points $(\mathbf{x} | \boldsymbol{\theta})$ where one or more of the x_k 's is zero. Those represent trajectories where some types are permanently extinct. The vector of resource variables $\boldsymbol{\theta}$ takes values in a torus, which has no inherent topological boundary, so all possible values of all θ_k 's are permitted for points in $\partial \mathscr{X}^K$.

Note that if, on a trajectory, a particular x_j is always 0, then the differential equation for the corresponding resource Eq. (11) decouples from the rest of the dynamics and reduces to

$$\dot{oldsymbol{ heta}}_{j} = a imes \left(\cos \left(oldsymbol{ heta}_{j} + oldsymbol{\gamma}
ight) - \cos oldsymbol{\gamma}
ight)$$

which is equivalent to Eq. (8) after a change of timescale. In such circumstances, there are two equilibrium values for θ_j , -2γ and 0, and most trajectories will converge to the stable equilibrium at 0.

II. PHASE PORTRAITS AND BIFURCATIONS

A. Solving for interior fixed points

In this section, we focus on the interior of the phase space, that is, points $(\mathbf{x} | \boldsymbol{\theta})$ for which $\dot{\mathbf{x}} = 0$ and $\dot{\boldsymbol{\theta}} = 0$ as in Eqs. (10) to (11), and for which no x_k is zero. Away from $\partial \mathscr{X}^K$, for all k, $0 < x_k < 1$, in which case setting $\dot{x}_k = 0$ forces every θ_k to satisfy $\cos \theta_k = \phi$. Thus the θ_k 's take on at most two distinct values $\pm \arccos \phi$ for each possible value of ϕ .

Setting $\dot{\theta}_k = 0$ in Eq. (11) and isolating x_k yields

$$x_k = \frac{\cos\left(\theta_k + \gamma\right) - \cos\gamma}{\beta} \tag{12}$$

The constraint $0 < x_k < 1$ forces

 $0 < \cos\left(\theta_k + \gamma\right) - \cos\gamma < \beta$



Figure 3. Graph of $g(\theta) = \cos(\theta + \gamma) - \cos \gamma$ as a function of θ for the example case of $\gamma = \pi/4$. Note that $g(\theta) > 0$ between the zero crossings at -2γ and 0.

which forces θ_k to be between -2γ and 0 (see Fig. 3).

Since θ_k must be negative, it must be the case that $\theta_k \cong -\arccos \phi$. Furthermore, $-\pi < -2\gamma < \theta_k$, so $\sin \theta_k = -\sqrt{1 - \phi^2}$. The only possible value for x_k as in Eq. (12) is now fixed. It may be re-expressed using the sum identity for cosine as follows,

$$x_{k} = \frac{\cos \theta_{k} \cos \gamma - \sin \theta_{k} \sin \gamma - \cos \gamma}{\beta}$$

$$= \frac{\phi \cos \gamma + \sqrt{1 - \phi^{2}} \sin \gamma - \cos \gamma}{\beta}.$$
(13)

Since all of the x_k 's are equal and must sum to 1, we get $x_k = 1/K$. Incorporating this into Eq. (13) results in

$$\phi \cos \gamma + \sqrt{1 - \phi^2} \sin \gamma - \cos \gamma = \frac{\beta}{K}$$

This equation can be solved by isolating $\sqrt{1-\phi^2}$ and squaring both sides, yielding a quadratic equation for ϕ . After simplification, its solutions are

$$\bar{\phi}_{\pm} = \cos\gamma \cdot \left(\cos\gamma + \frac{\beta}{K}\right) \pm \sin\gamma \cdot \sqrt{1 - \left(\cos\gamma + \frac{\beta}{K}\right)^2}$$
(14)

Let us also define

$$\hat{\phi}_{\pm} = \sqrt{1 - \bar{\phi}_{\pm}^2} = \sin \arccos \bar{\phi}_{\pm} \tag{15}$$

so that $\sin \theta_k = -\hat{\phi}_{\pm}$ at these fixed points.

Recalling that $0 < \gamma < \pi/2$, $\beta \ge 0$, and K > 0, the values of $\bar{\phi}_{\pm}$ in Eq. (14) are distinct and real when

$$0 \le \cos \gamma + \frac{\beta}{K} < 1. \tag{16}$$

It is useful to define

$$\beta_k^* = k(1 - \cos \gamma) \text{ for } 1 \le k \le K \tag{17}$$

so that Eq. (16) holds exactly when $\beta < \beta_K^*$. When $\beta = \beta_K^*$, the term under the square-root in Eq. (14) is zero, so $\bar{\phi}_+ = \bar{\phi}_-$, which results in a bifurcation in which the two fixed points collide and vanish as β increases. This turns out not to be a simple saddle-node bifurcation, but a much more degenerate bifurcation, described in Section II B.

Substituting $x_k = 1/\kappa$ into Eq. (12) and solving for θ_k results in

$$\boldsymbol{\theta}_k \cong -\boldsymbol{\gamma} \pm \boldsymbol{\delta} \tag{18}$$

where

$$\delta = \arccos\left(\cos\gamma + \frac{\beta}{K}\right) \in [0, \gamma] \tag{19}$$

or, equivalently,

$$\beta = K(\cos \delta - \cos \gamma) \in [0, \beta_K^*].$$
⁽²⁰⁾

The bounds on δ are consequences of the condition $\beta \leq \beta_K^*$ needed to ensure the existence of the two fixed points in question, and the fact that the arccos in Eq. (19) is a decreasing function. Since $0 \leq \gamma \pm \delta < \pi/2$,

$$\sin \theta_k = \sin(-\gamma \pm \delta) = -\hat{\phi}_{\pm}$$

To summarize, when $\beta < \beta_K^*$, there are two interior fixed points that will be named \mathbf{p}_{\pm} . For both, each $x_k = 1/K$, and the θ_k 's are all equal, taking on one of the two values $-\gamma \pm \delta \in [-2\gamma, 0]$.

At \mathbf{p}_{\pm} , for all k,

$$\begin{aligned} x_k &= \frac{1}{K} \\ \theta_k &= -\gamma \pm \delta \\ \phi &= \bar{\phi}_{\pm} \\ \hat{\phi}_{\pm} &= \sqrt{1 - \bar{\phi}_{\pm}^2} \\ \cos \theta_k &= \cos(-\gamma \pm \delta) = \bar{\phi}_{\pm} \\ \sin \theta_k &= \sin(-\gamma \pm \delta) = -\hat{\phi}_{\pm}. \end{aligned}$$

B. Linear stability analysis of interior fixed points

In this subsection, we calculate the Jacobian matrix and its eigenvalues and eigenvectors at \mathbf{p}_{\pm} . The calculations are simpler using the extended phase space method. The constraint that $\sum_{k} x_{k} = 1$ is suspended, and all the x_{k} 's are considered to be independent. It is then possible to treat \mathscr{X}^{K} as an invariant manifold within an enlarged phase space $\mathbb{R}^{K} \times \mathscr{T}^{K}$.

Let us express the dynamics in terms of vector functions \mathbf{f} and \mathbf{g}

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \boldsymbol{\theta})$$

 $\dot{\boldsymbol{\theta}} = \mathbf{g}(\mathbf{x}, \boldsymbol{\theta})$

where

$$f_k(\mathbf{x}, \boldsymbol{\theta}) = x_k \left(\cos \theta_k - \phi\right) \text{ and } \phi = \sum_j x_j \cos \theta_j$$
 (21)

$$g_k(\mathbf{x}, \boldsymbol{\theta}) = a\left(\cos\left(\theta_k + \gamma\right) - \cos\gamma - \beta x_k\right). \tag{22}$$

The necessary partial derivatives are taken assuming that all variables are independent, which yields

$$\frac{\partial f_k}{\partial x_j} = -x_k \cos \theta_j \text{ for } j \neq k$$
$$\frac{\partial f_k}{\partial x_k} = (1 - x_k) \cos \theta_k - \phi = -x_k \cos \theta_k + \cos \theta_k - \phi$$
$$\frac{\partial f_k}{\partial \theta_j} = x_k x_j \sin \theta_j \text{ for } j \neq k$$
$$\frac{\partial f_k}{\partial \theta_k} = -x_k (1 - x_k) \sin \theta_k$$

and

$$\frac{\partial g_k}{\partial x_j} = 0 \text{ for } j \neq k$$
$$\frac{\partial g_k}{\partial x_k} = -a\beta$$
$$\frac{\partial g_k}{\partial \theta_j} = 0 \text{ for } j \neq k$$
$$\frac{\partial g_k}{\partial \theta_k} = -a\sin(\theta_k + \gamma)$$

At the two fixed points, using $\bar{\phi}_{\pm}$ from Eq. (14) and $\hat{\phi}_{\pm}$ from Eq. (15),

$$\begin{aligned} \frac{\partial f_k}{\partial x_j} \Big|_{\mathbf{p}_{\pm}} &= -\frac{1}{K} \bar{\phi}_{\pm} \text{ for } j \neq k \\ \frac{\partial f_k}{\partial x_k} \Big|_{\mathbf{p}_{\pm}} &= -\frac{1}{K} \bar{\phi}_{\pm} \\ \frac{\partial f_k}{\partial \theta_j} \Big|_{\mathbf{p}_{\pm}} &= -\frac{1}{K^2} \hat{\phi}_{\pm} \text{ for } j \neq k \\ \frac{\partial f_k}{\partial \theta_k} \Big|_{\mathbf{p}_{\pm}} &= \frac{K-1}{K^2} \hat{\phi}_{\pm}. \end{aligned}$$
(23)

Furthermore,

$$\frac{\partial g_k}{\partial x_j}\Big|_{\mathbf{p}_{\pm}} = 0 \text{ for } j \neq k$$

$$\frac{\partial g_k}{\partial x_k}\Big|_{\mathbf{p}_{\pm}} = -a\beta$$

$$\frac{\partial g_k}{\partial \theta_j}\Big|_{\mathbf{p}_{\pm}} = 0 \text{ for } j \neq k$$

$$\frac{\partial g_k}{\partial \theta_k}\Big|_{\mathbf{p}_{\pm}} = -a\sin(\pm\delta).$$
(24)

Using **N** for a $K \times K$ matrix of all 1's and **I** for the $K \times K$ identity matrix, the partial derivatives at the fixed points as given in Eqs. (23) to (24) may be stacked to form a Jacobian matrix with block form

$$\mathbf{J}|_{\mathbf{p}_{\pm}} = \begin{bmatrix} -\frac{1}{K} \bar{\phi}_{\pm} \mathbf{N} \middle| \hat{\phi}_{\pm} \left(-\frac{1}{K^2} \mathbf{N} + \frac{1}{K} \mathbf{I} \right) \\ \hline \\ -a\beta \mathbf{I} \middle| -a\sin(\pm\delta) \mathbf{I} \end{bmatrix}.$$

Consider an eigenvector $(\mathbf{x} | \boldsymbol{\theta})$ with eigenvalue λ , that is,

$$\mathbf{J}|_{\mathbf{p}_{\pm}}\left[\frac{\mathbf{x}}{\boldsymbol{\theta}}\right] = \lambda \left[\frac{\mathbf{x}}{\boldsymbol{\theta}}\right].$$
(25)

The upper half of Eq. (25) yields

$$-\frac{1}{K}\bar{\phi}_{\pm}\mathbf{N}\mathbf{x} + \hat{\phi}_{\pm}\left(-\frac{1}{K^2}\mathbf{N} + \frac{1}{K}\mathbf{I}\right)\boldsymbol{\theta} = \lambda\mathbf{x}.$$
(26)

The lower half of Eq. (25) yields

$$\mathbf{x} = -\left(\frac{\lambda \pm a\sin\delta}{a\beta}\right)\boldsymbol{\theta}.$$
 (27)

Using Eq. (27) to substitute for x in Eq. (26) yields

$$\begin{pmatrix}
\frac{1}{K}\bar{\phi}_{\pm}\left(\frac{\lambda\pm a\sin\delta}{a\beta}\right) - \frac{1}{K^{2}}\hat{\phi}_{\pm}\right)\mathbf{N}\boldsymbol{\theta} \\
= \left(-\frac{1}{K}\hat{\phi}_{\pm} - \lambda\cdot\frac{\lambda\pm a\sin\delta}{a\beta}\right)\boldsymbol{\theta}.$$
(28)

This is effectively an equation for eigenvalues of **N**. By inspection, the eigenvalues of **N** are *K* with multiplicity 1, corresponding to the eigenvector 1; and 0 with multiplicity K - 1, corresponding to the eigenvectors $\mathbf{e}_{k+1} - \mathbf{e}_k$ for k = 1, ..., K - 1. (The notation \mathbf{e}_j refers to the elementary basis vector in which element *j* is 1 and all others are 0.) Each of these yields two eigenvalues for $\mathbf{J}|_{\mathbf{p}_{\pm}}$ with corresponding multiplicities and eigenvectors. These eigenvalues will be named λ_{\pm}^{ℓ} with $\ell \in \{T, U, Y, Z\}$. The letter serves as a tag to distinguish eigenvalues associated with the same fixed point. The subscript sign (+ or -) indicates which fixed point (\mathbf{p}_+ or \mathbf{p}_-) the eigenvalue is associated with. The corresponding eigenvectors will be named \mathbf{v}_{\pm}^{ℓ} using the same convention.

The eigenvalues λ_{\pm}^{T} and λ_{\pm}^{U} for $\mathbf{J}|_{\mathbf{p}_{\pm}}$ are derived from the eigenvalue *K* of **N**. Substituting $\boldsymbol{\theta} = \mathbf{1}$ into Eq. (28) and simplifying, each row becomes

$$\left(\bar{\phi}_{\pm}+\lambda\right)\left(rac{\lambda\pm a\sin\delta}{aeta}
ight)=0.$$

Solving for λ yields two eigenvalues of **J** of multiplicity 1,

$$\lambda_{\pm}^{\mathrm{T}} = -\bar{\phi}_{\pm} \text{ and } \lambda_{\pm}^{\mathrm{U}} = \mp a \sin \delta.$$

The corresponding eigenvectors are

$$\mathbf{v}_{\pm}^{\mathrm{T}} = \begin{bmatrix} -\frac{-\bar{\phi}_{\pm} \pm a \sin \delta}{a\beta} \\ \vdots \\ \hline 1 \\ \vdots \end{bmatrix} \text{ and } \mathbf{v}_{\pm}^{\mathrm{U}} = \begin{bmatrix} 0 \\ \vdots \\ 1 \\ \vdots \\ \vdots \end{bmatrix},$$

which may be found by substituting for λ in Eq. (27).

When using the extended phase space, the right-hand side of Eq. (3) is interpreted as a vector field on all of \mathbb{R}^{K} . The biologically interpretable points lie in $\mathscr{S}^{K} \subset \mathscr{H}$. Within that framework, one can determine the stability of a biologically interpretable fixed point $\bar{\mathbf{x}} \in \mathscr{S}^{K}$ considering only the behavior of nearby orbits within \mathscr{S}^{K} , but not those outside. In that case, initial conditions of the form $\bar{\mathbf{x}} + \mathbf{u}$ are of interest only if $\mathbf{u} \cdot \mathbf{1} = 0$, a consequence of imposing the constraint $\bar{\mathbf{x}} + \mathbf{u} \in \mathscr{H}$, which amounts to $(\bar{\mathbf{x}} + \mathbf{u}) \cdot \mathbf{1} = 1$. Thus, given a Jacobian matrix for the extended dynamics, only eigenvectors \mathbf{u} that satisfy $\mathbf{u} \cdot \mathbf{1} = 0$ are relevant. For replicator-resource dynamics, that means an eigenvector $\mathbf{v} = (\mathbf{u} \mid \boldsymbol{\zeta})$ is relevant only if $\mathbf{u} \cdot \mathbf{1} = 0$. Examining $\mathbf{v}_{\pm}^{T} = (\mathbf{u}_{\pm}^{T} \mid \boldsymbol{\zeta}_{\pm}^{T}), \mathbf{u}_{\pm}^{T}$ is a scalar multiple of $\mathbf{1}$, so $\mathbf{u}_{\pm}^{T} \cdot \mathbf{1} \neq 0$ and it points out of \mathscr{H} . Therefore, the corresponding eigenvalue λ_{\pm}^{T} is not of interest.

Note that the fixed points \mathbf{p}_{\pm} only exist when $\beta < \beta_K^*$, in which case the bounds on δ from Eq. (19) imply that λ_{\pm}^U must be real.

The eigenvalues λ_{\pm}^{Y} and λ_{\pm}^{Z} for $\mathbf{J}|_{\mathbf{p}_{\pm}}$ are derived from the eigenvalue 0 of **N**. Consider $\mathbf{N}\boldsymbol{\theta} = \mathbf{0}$ with $\boldsymbol{\theta} = \mathbf{e}_{k+1} - \mathbf{e}_{k}$. Substituting into Eq. (28) results in a quadratic equation in λ ,

$$-\frac{1}{K}\hat{\phi}_{\pm} - \lambda \cdot \frac{\lambda \pm a\sin\delta}{a\beta} = 0$$

or

$$K\lambda^2 \pm (Ka\sin\delta)\lambda + a\beta\hat{\phi}_{\pm} = 0.$$
⁽²⁹⁾

Since $a, K, \hat{\phi}_{\pm}$, and β are all positive, both roots have the same sign when they are real. The roots are

$$\lambda_{\pm}^{\mathbf{Y}} = \mp \frac{a\sin\delta}{2} - \frac{\sqrt{(Ka\sin\delta)^2 - 4Ka\hat{\phi}_{\pm}\beta}}{2K}$$
$$\lambda_{\pm}^{\mathbf{Z}} = \mp \frac{a\sin\delta}{2} + \frac{\sqrt{(Ka\sin\delta)^2 - 4Ka\hat{\phi}_{\pm}\beta}}{2K}.$$

In all cases, the real parts of λ_{-}^{Y} and λ_{-}^{Z} are positive, and the real parts of λ_{+}^{Y} and λ_{+}^{Z} are negative.

Each of λ_{\pm}^{Y} and λ_{\pm}^{Z} inherits the multiplicity K - 1. The corresponding eigenvectors \mathbf{v}_{\pm}^{Y} and \mathbf{v}_{\pm}^{Z} are built by stacking $\boldsymbol{\theta} = \mathbf{e}_{k+1} - \mathbf{e}_{k}$ with the **x** component determined from Eq. (27).

When $\beta < \beta_K^*$, the fixed points \mathbf{p}_{\pm} exist and are distinct. The fixed point \mathbf{p}_+ is a sink because the relevant eigenvalues, λ_+^U , λ_+^Y , and λ_+^Z , all have negative real parts. Likewise, \mathbf{p}_- is a source because all of its relevant eigenvalues have positive real parts.

The discriminant Δ_{\pm} of Eq. (29) can be expressed in terms of δ by using Eq. (20) to substitute

for β ,

$$\Delta_{\pm} = (Ka\sin\delta)^2 - 4Ka\hat{\phi}_{\pm}\beta$$
$$= K^2a \left(a\sin^2\delta + 4(\cos\delta - \cos\gamma)\sin(\pm\delta - \gamma)\right)$$

Its sign determines whether λ_{\pm}^{Y} and λ_{\pm}^{Z} are real or complex, and when expressed in terms of δ , this sign is independent of the number of types *K*. If $\beta = 0$, then $\delta = \gamma$ and

$$\Delta_{\pm}|_{\beta=0} = K^2 a^2 \sin^2 \gamma > 0,$$

so for small values of β , these eigenvalues are real. If $\beta = \beta_K^*$, then $\delta = 0$ and

$$\Delta_{\pm}|_{\beta=\beta_K^*}=-4K^2a(1-\cos\gamma)\sin\gamma<0,$$

so for large values of β , these eigenvalues are complex. By the intermediate value theorem, there must be a δ between 0 and γ at which $\Delta_{\pm} = 0$. Using a computer algebra system such as Mathematica, it is possible to solve the equation $\Delta_{\pm} = 0$ for the value of δ at which the eigenvalues become complex. The resulting expression is unwieldy and difficult to interpret, so it will not be presented. Importantly, since the transition occurs at some $\delta > 0$, the real components of λ_{\pm}^{Y} and λ_{\pm}^{Z} are nonzero, so there is no Hopf-like bifurcation.

If $\beta = \beta_K^*$, then $\delta = 0$ and $\mathbf{p}_+ = \mathbf{p}_-$. Furthermore, $\lambda_{\pm}^U = 0$, and both λ_{\pm}^Y and λ_{\pm}^Z are purely imaginary, so a degenerate saddle-node bifurcation occurs as β crosses β_K^* .

C. Fixed points on the boundary in the case of K = 2

We focus now on the low-dimensional case of K = 2. In this subsection, we use the reduced system method. Starting from Eqs. (10) to (11) and eliminating x_2 with the constraint $x_2 = 1 - x_1$, the dynamics are

$$\dot{x}_1 = x_1(1 - x_1)(\cos\theta_1 - \cos\theta_2)$$

$$\dot{\theta}_1 = a(\cos(\theta_1 + \gamma) - \cos\gamma - \beta x_1)$$

$$\dot{\theta}_2 = a(\cos(\theta_2 + \gamma) - \cos\gamma - \beta(1 - x_1)).$$
(30)



Figure 4. Representation of \mathscr{X}^2 as a thickened torus \mathscr{D} . The inner shell is the set of points where $x_1 = 0$. The outer shell is the set of points where $x_1 = 1$. The dashed circle on the outer shell going through the central hole is the set of points where $x_1 = 1$ and $\theta_2 = 0$. The dashed circle around the outer shell represents points where $x_1 = 1$ and $\theta_1 = 0$. Arrows indicate the increasing direction of each variable. The interior fixed points \mathbf{p}_+ and \mathbf{p}_- are indicated by dots.

The three-dimensional \mathscr{X}^2 can be identified with a thickened torus. For this article, a specific thickened torus, $\mathscr{D} \subset \mathbb{R}^3$, will be used:

$$\mathscr{D} = \left\{ \mathbf{R}_{12} \left(\theta_2 \right) \left(\begin{bmatrix} 2\\0\\0 \end{bmatrix} + \mathbf{R}_{13} \left(\theta_1 \right) \begin{bmatrix} \frac{1}{2} + x_1\\0\\0 \end{bmatrix} \right)$$

$$\left| 0 \le x_1 \le 1, \theta_k \in \mathscr{T}^1 \right\}$$

$$(31)$$

where $\mathbf{R}_{mn}(\theta)$ means rotation by θ in the $(\mathbf{e}_m, \mathbf{e}_n)$ plane. Overall, \mathscr{D} is built by rotating an annulus in the $(\mathbf{e}_1, \mathbf{e}_3)$ plane around a circle in the $(\mathbf{e}_1, \mathbf{e}_2)$ plane. In Eq. (31), \mathscr{D} is defined in terms of a bijection that maps each point $(x_1, 1 - x_1 | \theta_1, \theta_2) \in \mathscr{X}^2$ to a point in \mathscr{D} as follows. Begin with $(1/2 + x_1)\mathbf{e}_1$. Rotate that point through the angle θ_1 about the origin in the $(\mathbf{e}_1, \mathbf{e}_3)$ plane. As x_1 ranges over [0, 1] and θ_1 ranges over its circle, that step results in an annulus centered at the origin, with inner radius 1/2 and outer radius 3/2. The annulus is then translated out so that it is centered at $2\mathbf{e}_1$, then rotated by θ_2 in the $(\mathbf{e}_1, \mathbf{e}_2)$ plane. See Fig. 4 for a visual explanation of the resulting coordinate system.

The outer shell of $\partial \mathscr{X}^2$ consists of points where $x_1 = 1$ and $x_2 = 0$, that is, strategy 2 is permanently missing, so the entire population uses strategy 1. Trajectories passing through such

points are confined to the outer shell. Only θ_1 and θ_2 are changing, and their dynamics decouple into

$$\dot{\theta}_1 = a \cdot (\cos(\theta_1 + \gamma) - \cos\gamma - \beta)$$

$$\dot{\theta}_2 = a \cdot (\cos(\theta_2 + \gamma) - \cos\gamma).$$
(32)

The solutions to $\dot{\theta}_2 = 0$ are 0 and -2γ , which may be represented as

$$\theta_2 \cong -\gamma \pm \gamma.$$
 (33)

The solutions to $\dot{\theta}_1 = 0$ are

$$\theta_1 \cong -\gamma \pm \omega$$
 where $\omega = \arccos(\cos \gamma + \beta)$ (34)

Both solutions for θ_1 exist and are distinct if $\beta < 1 - \cos \gamma = \beta_1^*$, and coincide when $\beta = \beta_1^*$.

Thus, for $\beta < \beta_1^*$, there are four fixed points on the outer shell of $\partial \mathscr{X}^2$. They are found by mixing the two choices of θ_1 from Eq. (34) with the two choices of θ_2 from Eq. (33). The choice for each θ_j amounts to choosing a sign s_j . The fixed points will be named $\mathbf{q}_1(s_1, s_2)$ with the two signs as arguments. Their components $(x_1, x_2 | \theta_1, \theta_2)$ are

$$\mathbf{q}_1(s_1,s_2) = (1,0 | -\gamma + s_1 \boldsymbol{\omega}, -\gamma + s_2 \gamma)$$
 where $s_j = \pm 1$.

There are parallel fixed points on the inner shell of $\partial \mathscr{X}^2$,

$$\mathbf{q}_{2}(s_{1},s_{2}) = (0,1 | -\gamma + s_{1}\gamma, -\gamma + s_{2}\omega)$$
 where $s_{j} = \pm 1$.

The arccos function is decreasing, so from the definition of ω in Eq. (34),

$$0 \le \omega \le \gamma < \frac{\pi}{2}.$$
(35)

If $\beta = \beta_1^*$, then $\omega = 0$, which results in

$$\mathbf{q}_{1}(-1, s_{2}) = \mathbf{q}_{1}(1, s_{2}) = (1, 0 | -\gamma, -\gamma + s_{2}\gamma)$$
$$\mathbf{q}_{2}(s_{1}, -1) = \mathbf{q}_{2}(s_{1}, 1) = (0, 1 | -\gamma + s_{1}\gamma, -\gamma).$$

That is, two pairs of fixed points collide. When $\beta > \beta_1^*$, there is no real value for ω , so none of these fixed points exist. Thus, a pair of saddle-node bifurcations happen simultaneously at $\beta = \beta_1^*$.

D. Linear stability analysis of fixed points on the boundary in the case of K = 2

The linear stability analysis of the fixed points from Section II C is best conducted in three dimensions, using the reduced system method, fixing $x_2 = 1 - x_1$. The Jacobian matrix for Eq. (30) in the three variables x_1 , θ_1 , and θ_2 is

$$\mathbf{J} = \begin{bmatrix} (1-2x_1)(\cos\theta_1 - \cos\theta_2) & -x_1(1-x_1)\sin\theta_1 & x_1(1-x_1)\sin\theta_2 \\ & -a\beta & -a\sin(\theta_1 + \gamma) & 0 \\ & a\beta & 0 & -a\sin(\theta_2 + \gamma) \end{bmatrix}$$

At the fixed point $\mathbf{q}_1(s_1, s_2)$,

$$\mathbf{J}|_{\mathbf{q}_1} = \begin{bmatrix} \cos(\gamma - s_2 \gamma) - \cos(\gamma - s_1 \omega) & 0 & 0 \\ -a\beta & -as_1 \sin \omega & 0 \\ a\beta & 0 & -as_2 \sin \gamma \end{bmatrix}.$$

Since this matrix is in lower triangular form, the eigenvalues can be read off the diagonal. They will be named λ^{ℓ} where $\ell \in \{A, B, C\}$, where the letter serves as a tag to distinguish them. Each is expressed as a function of one or two of the signs used to specify \mathbf{q}_1 .

$$\lambda^{A}(s_{1}, s_{2}) = \cos(\gamma - s_{2}\gamma) - \cos(\gamma - s_{1}\omega)$$
$$\lambda^{B}(s_{1}) = -as_{1}\sin\omega$$
$$\lambda^{C}(s_{2}) = -as_{2}\sin\gamma.$$

Convenient eigenvectors are

$$\mathbf{v}^{\mathrm{A}} = (\mathbf{e}_{1} | \mathbf{0})$$
$$\mathbf{v}^{\mathrm{B}} = (\mathbf{0} | \mathbf{e}_{1})$$
$$\mathbf{v}^{\mathrm{C}} = (\mathbf{0} | \mathbf{e}_{2}).$$

From Eq. (35) and assuming $0 < \beta < \beta_1^*$ and $\gamma < \pi/2$,

$$\begin{split} \lambda^B(-1) &> 0, \ \lambda^B(1) < 0, \\ \lambda^C(-1) &> 0, \ \lambda^C(1) < 0, \end{split}$$

and

$$\begin{split} \lambda^{A}(-1,-1) &= \cos 2\gamma - \cos(\gamma + \omega) < 0, \\ \lambda^{A}(-1,1) &= 1 - \cos(\gamma + \omega) > 0, \\ \lambda^{A}(1,-1) &= \cos 2\gamma - \cos(\gamma + \omega) < 0, \\ \lambda^{A}(1,1) &= 1 - \cos(\gamma - \omega) > 0. \end{split}$$

Thus, all the fixed points are saddles: $\mathbf{q}_1(-1,-1)$ has one negative eigenvalue and two positive; $\mathbf{q}_1(-1,1)$ has one negative and two positive; $\mathbf{q}_1(1,-1)$ has two negative and one positive; $\mathbf{q}_1(1,1)$ has two negative and one positive. If $\boldsymbol{\beta} = \boldsymbol{\beta}_1^*$, then $\lambda^{\mathrm{B}}(s_1) = 0$, consistent with the pair of saddle-node bifurcations noted in Section II C.

Recall that the dynamics given by Eqs. (10) to (11) are symmetric under parallel permutations of the x_k 's and θ_k 's. This translates into the fact that the dynamics in Eq. (30) are symmetric under the transformation $x_1 \leftrightarrow 1 - x_1$ and $\theta_1 \leftrightarrow \theta_2$. Consequently, the fixed points on the inner shell, given by $x_1 = 0$, have behavior exactly parallel to that of the fixed points on the outer shell given by $x_1 = 1$.

E. Fixed points on the boundary for K > 2

When K > 2, many of the results of Sections II C and II D can be generalized. This is accomplished by taking advantage of the fact that $\partial \mathscr{X}^K$ consists of lower-dimensional simplices. Now that *K* is allowed to be greater than 2, we return to the extended phase space method of analysis.

1. When one $x_k = 1$

Calculations in this section are the first step to generalizing those of Sections IIC and IID to K > 2. On each part of $\partial \mathscr{X}^K$ such that there is one k for which $x_k = 1$, the dynamics fix x_k at 1 while the other x_j 's are permanently zero. Due to the symmetries of the dynamics, it is only necessary to analyze the case of k = K, so any fixed points satisfy $\mathbf{x} = \mathbf{e}_K$. The remaining fixed-point equations come from setting $\dot{\theta}_j = 0$ in Eq. (11) and substituting $\mathbf{x} = \mathbf{e}_K$,

$$0 = a(\cos(\theta_K + \gamma) - \cos\gamma - \beta)$$

$$0 = a(\cos(\theta_j + \gamma) - \cos\gamma) \text{ for } 1 \le j < K.$$

The solutions are

$$\theta_{K} \cong -\gamma + s_{K}\omega \text{ where } \omega = \arccos\left(\cos\gamma + \beta\right)$$

$$\theta_{j} \cong -\gamma + s_{j}\gamma \text{ for } 1 \le j < K,$$
(36)

where each $s_j = -1$ or 1. Consequently, there are 2^K fixed points, one for each combination of values for all the s_j 's. Generalizing the notation from Section II C, they will be denoted $\mathbf{q}_k(\mathbf{s})$ with the subscript indicating the *k* for which $x_k = 1$,

$$\mathbf{q}_k(\mathbf{s}) = \left(\mathbf{e}_k \left| (-\gamma + s_k \boldsymbol{\omega}) \mathbf{e}_k + \sum_{j \neq k} (-\gamma + s_j \gamma) \mathbf{e}_j \right).$$

For linear stability analysis, we will use the extended phase space and Jacobian matrix, as in Section II B. Again, due to symmetry, we need only consider \mathbf{q}_K . It is best to break up the Jacobian into blocks,

$$\mathbf{J}|_{\mathbf{q}_{K}} = \begin{bmatrix} \mathbf{E} & \mathbf{0} \\ \\ -a\beta\mathbf{I} & \mathbf{F} \end{bmatrix},\tag{37}$$

where E is diagonal except for the last row,

$$\mathbf{E} = \begin{bmatrix} \cos \theta_1 - \cos \theta_K & 0 & \dots & 0 \\ 0 & \cos \theta_2 - \cos \theta_K & \vdots \\ \vdots & \ddots & 0 \\ \hline -\cos \theta_1 & -\cos \theta_2 & \dots & -\cos \theta_K \end{bmatrix}$$

and **F** is diagonal,

$$\mathbf{F} = \begin{vmatrix} -a\sin(\theta_1 + \gamma) & 0 & \dots \\ 0 & -a\sin(\theta_2 + \gamma) \\ \vdots & \ddots \end{vmatrix}.$$

The eigenvalues of $\mathbf{J}|_{\mathbf{q}_K}$ will be named λ_j^{ℓ} , where the letter $\ell \in \{E, F\}$ is a tag that indicates which part of the matrix in Eq. (37) the eigenvalue is read from, and $j \in \{1, \dots, K\}$. The corresponding eigenvectors will be named \mathbf{v}_j^{ℓ} using the same convention.

Since this Jacobian is for the extended phase space, there should be one spurious eigenvector whose **x**-component points out of the plane \mathcal{H} . In this case, it is

$$\mathbf{v}_{K}^{\mathrm{E}} = \left(\left(\frac{\cos \theta_{K} - a \sin(\theta_{K} + \gamma)}{a \beta} \right) \mathbf{e}_{K} \, \middle| \, \mathbf{e}_{K} \right)$$

associated with the bottom-right entry of **E**, namely, $\lambda_K^E = -\cos \theta_K$. Thus, the eigenvalue λ_K^E is not relevant to the linear stability analysis of fixed points within \mathscr{X}^K . For additional confirmation, note that this eigenvalue has no analog in Section II D, in which the spectrum of the Jacobian was calculated using the reduced system method.

Substituting for $\boldsymbol{\theta}$ with Eq. (36),

$$\lambda_{j}^{\mathrm{E}}(\mathbf{s}) = \cos(-\gamma + s_{j}\gamma) - \cos(-\gamma + s_{K}\omega) \text{ for } 1 \le j < K$$

$$\lambda_{j}^{\mathrm{F}}(\mathbf{s}) = -as_{j}\sin\gamma \text{ for } 1 \le j < K$$

$$\lambda_{K}^{\mathrm{F}}(\mathbf{s}) = -as_{K}\sin\omega.$$
(38)

The eigenvectors $\mathbf{v}_j^{\mathrm{F}}(\mathbf{s})$ are easily seen to be $(\mathbf{0} | \mathbf{e}_j)$. To recover the other eigenvectors, substitute the form $\mathbf{v}_j^{\mathrm{E}}(\mathbf{s}) = (c(\mathbf{e}_j - \mathbf{e}_K) | d\mathbf{e}_j + \mathbf{e}_K)$ for \mathbf{v} in $\mathbf{J}\mathbf{v} = (\cos\theta_j - \cos\theta_K)\mathbf{v}$, where *c* and *d* are unknowns to be solved for. The **x**-component of that equation holds for every *c*. The $\boldsymbol{\theta}$ -component requires

$$-a\beta c - a\sin(\theta_K + \gamma) = \cos\theta_j - \cos\theta_K$$
$$a\beta c - da\sin(\theta_j + \gamma) = (\cos\theta_j - \cos\theta_K)d$$

which yields

$$c = -\frac{\cos \theta_j - \cos \theta_K + a \sin(\theta_K + \gamma)}{a\beta}$$
$$d = -\frac{\cos \theta_j - \cos \theta_K + a \sin(\theta_K + \gamma)}{\cos \theta_j - \cos \theta_K + a \sin(\theta_j + \gamma)}$$

Then substitute for $\boldsymbol{\theta}$ using Eq. (36). The resulting expression for $\mathbf{v}_j^{\text{E}}(\mathbf{s})$ is large and not needed, so it will not be displayed here.

The eigenvalues λ_j^{ℓ} in Eq. (38) are always real. Assuming $0 < \beta < \beta_1^*$ and $\gamma < \pi/2$, from Eq. (35), the same reasoning as in Section II D implies that for all *j*,

$$\operatorname{sgn}\lambda_j^{\mathrm{F}}(\mathbf{s}) = -s_j.$$

Furthermore,

$$\operatorname{sgn}\lambda_j^{\mathrm{E}}(\mathbf{s}) = s_j$$

So these fixed points are all saddles.

For different choices of **s**, the fixed points $\mathbf{q}_k(\mathbf{s})$ are generally distinct unless $\beta = \beta_1^*$, in which case $\omega = 0$, and pairs of fixed points that differ at only one element of **s** collide. The result is many simultaneous saddle-node bifurcations that result in the elimination of all fixed points $\mathbf{q}_k(\mathbf{s})$.

2. When some subset of x_k 's are all 0

Given 1 < L < K, consider the subset \mathscr{X}^L of \mathscr{X}^K consisting of the points $(\mathbf{x} | \boldsymbol{\theta})$ for which $x_{L+1} = 0, x_{L+2} = 0, \dots, x_K = 0$. Then \mathscr{X}^L can be interpreted as the phase space of an *L*-strategy version of the same game dynamics on x_1, \dots, x_L and $\theta_1, \dots, \theta_L$, with the remaining x_k pinned permanently at 0 and corresponding θ_k variables decoupled. As a base case, the analysis of \mathscr{X}^2 is exactly as presented in Sections II C, II D and II E 1. For higher values of *K*, the analysis proceeds inductively as follows.

Consider K = 3 and the subset of \mathscr{X}^3 where $x_3 = 0$. The resource variable θ_3 is now decoupled from the other variables, whose dynamics are otherwise the same as those of replicator-resource dynamics with K = 2. Therefore, every fixed point for K = 3 on the face of $\partial \mathscr{X}^3$ where $x_3 = 0$ is of the form $(x_1, x_2, 0 | \theta_1, \theta_2, -\gamma + s_3 \gamma)$ with $s_3 = \pm 1$, corresponding to a fixed point $(x_1, x_2 | \theta_1, \theta_2)$ under replicator-resource dynamics with K = 2. Conversely, all fixed points on the face of $\partial \mathscr{X}^3$ where $x_3 = 0$ may be found by starting with the fixed points $(x_1, x_2 | \theta_1, \theta_2)$ found in Sections II A and IIC, and extending them with $x_3 = 0$ and $\theta_3 \cong -\gamma + s_3 \gamma$ with $s_3 = \pm 1$. The extension with $s_3 = 1$ sets $\theta_3 \cong 0$, so x_3 would increase if perturbed away from 0, resulting in an unstable fixed point in $\partial \mathscr{X}^3$. The extension with $s_3 = -1$ sets $\theta_3 \cong -2\gamma$, which is unstable in θ_3 , likewise resulting in an unstable fixed point in $\partial \mathscr{X}^3$.

The fixed points $\mathbf{q}_j(s_1, s_2)$ found in Section II C all vanish in simultaneous saddle-node bifurcations as β increases through β_1^* , so the same happens to their extensions in $\partial \mathscr{X}^3$. Likewise, the fixed points \mathbf{p}_{\pm} found in Section II A on the interior of \mathscr{X}^2 vanish in simultaneous bifurcations as β increases through β_2^* , so the same happens to their extensions in $\partial \mathscr{X}^3$.

The same reasoning applies for the dynamics restricted to any choice of two indices out of $\{1,2,3\}$ for the x_j 's that are allowed to be non-zero. Overall, the result is a variety of saddles and sources on the boundary of \mathscr{X}^3 that collide and vanish as β increases. The ones with one non-zero **x**-element vanish when $\beta = \beta_1^*$. The ones with two non-zero **x**-elements vanish when $\beta = \beta_2^*$. The two fixed points \mathbf{p}_{\pm} in the interior of \mathscr{X}^3 collide and vanish when $\beta = \beta_3^*$.

The same reasoning can be applied iteratively. In general, the boundary of \mathscr{X}^{K} contains many sources and saddles, and the ones for which *L* of the **x**-elements are non-zero collide and vanish when $\beta = \beta_{L}^{*}$. The last two surviving fixed points are a source \mathbf{p}_{-} and a sink \mathbf{p}_{+} on the interior of \mathscr{X}^{K} . The sink \mathbf{p}_{+} is the only stable fixed point for any choice of β .

F. Global consequences of the bifurcation at $\beta = \beta_1^*$

We consider the case of general *K*, using the case of K = 2 and the representation of \mathscr{X}^2 as \mathscr{D} as in Eq. (31) for illustration purposes. There is an important global change of behavior as β increases through β_1^* . Observe from Eq. (11) that as long as

$$\beta < \beta_1^* = 1 - \cos \gamma$$

there is an interval on each θ_k 's circle of possible values for which $\dot{\theta}_k > 0$ no matter what x_k is. Formally, starting with Eq. (10), and assuming $\beta = \beta_1^* - \varepsilon$, any value of **x** results in

$$\frac{1}{a}\dot{\theta}_{k} \geq \cos\left(\theta_{k}+\gamma\right) - \cos\gamma - \left(\beta_{1}^{*}-\varepsilon\right)$$
$$= \cos\left(\theta_{k}+\gamma\right) - \left(1-\varepsilon\right),$$

which is positive for θ_k in an interval around $-\gamma$. The existence of this interval prevents trajectories from whirling clockwise around the θ_k circle.

In the case of K = 2, this means trajectories can neither whirl around the central hole of \mathscr{D} nor through it. The intervals in question appear as sectors of the thickened torus that lie entirely between the nullclines \mathscr{N}_k^{θ} of the resource variables,

$$\mathscr{N}_{k}^{\theta} = \left\{ \left(\mathbf{x} \,|\, \boldsymbol{\theta} \right) \in \mathscr{X}^{K} \,\middle|\, \dot{\boldsymbol{\theta}}_{k} = 0 \right\}.$$
(39)

When $\beta < \beta_1^*$, these nullclines stretch from the inner shell of \mathcal{D} , where $x_1 = 0$, to the outer shell, where $x_1 = 1$. See Fig. 5.

To confirm this in general, let S_k be the subset $\partial \mathscr{X}^K$ where $x_k = 1$. (In the case of $K = 2, S_1$ is the outer shell of $\partial \mathscr{D}$ and S_2 is the inner shell.) Consider the intersection of S_k and the nullcline \mathscr{N}_k^{θ} . Setting $\dot{\theta}_k = 0$ from Eq. (11), substituting $x_k = 1$, and eliminating the factor of *a* yields

$$0 = \cos(\theta_k + \gamma) - \cos\gamma - \beta.$$
(40)

The graph of the right-hand side looks like Fig. 3 but shifted down by β .

If $\beta < \beta_1^* = 1 - \cos \gamma$, then solving Eq. (40) for θ_k yields two solutions, $\theta_k \cong -\gamma \pm \omega$ as in Eq. (36). The other θ_j 's for $j \neq k$ range over their whole circles. Therefore, \mathcal{N}_k^{θ} meets S_k in two (K-1)-dimensional tori.

If $\beta = \beta_1^*$, then $\omega = 0$ and there is only the one solution $\theta_k = -\gamma$. Effectively, the two tori merge, and \mathcal{N}_k^{θ} is tangent to S_k along that one (K-1)-dimensional torus.



Figure 5. Nullclines before the bifurcation, $\beta < \beta_1^*$. Parameters: $\beta = 0.2$, a = 1, $\gamma = \pi/4$. Subfigures (a) and (b): Two views of \mathcal{N}_1^{θ} as in Eq. (39). Subfigures (c) and (d): Two views of \mathcal{N}_2^{θ} as in Eq. (39).



Figure 6. Nullclines at the bifurcation at $\beta = \beta_1^*$. Parameters: $\beta = 1 - 1/\sqrt{2} \approx 0.292893$, a = 1, $\gamma = \pi/4$. Subfigures (a) and (b): Two views of \mathcal{N}_1^{θ} as in Eq. (39). The two pieces seen in Fig. 5 have merged into one piece tangent to the outer shell along a circle. Subfigures (c) and (d): Two views of \mathcal{N}_2^{θ} as in Eq. (39). Again, the two pieces have merged and the single surface is tangent to the inner shell.



Figure 7. Nullclines after the bifurcation, $\beta > \beta_1^*$. Parameters: $\beta = 0.4$, a = 1, $\gamma = \pi/4$. Subfigures (a) and (b): Two views of the θ_1 nullcline. It has detached from the outer shell. Subfigures (c) and (d): Two views of the θ_2 nullcline. It has detached from the inner shell.

If $\beta > \beta_1^*$, then there is no solution to Eq. (40) for θ_k . Now \mathscr{N}_k^{θ} is detached from S_k , leaving room for θ_k to decrease indefinitely. For illustration purposes, let us return to the low-dimensional case of K = 2. See Fig. 6 for the nullclines at this bifurcation ($\beta = \beta_1^*$), and Fig. 7 for the nullclines afterward ($\beta > \beta_1^*$). Note how the two components of the nullclines merge and partially detach from $\partial \mathscr{D}$, leaving a gap where trajectories can whirl. This restructuring of the nullclines causes the bifurcations in which fixed points on $\partial \mathscr{D}$ collide and vanish. On the outer shell of $\partial \mathscr{D}$, the dynamics of θ_1 and θ_2 reduce to Eq. (32), so once $\beta > \beta_1^*$, there are no solutions to $\dot{\theta}_1 = 0$ there; instead, $\dot{\theta}_1 < 0$ always, so all trajectories on the outer shell whirl through the central hole without stopping. Likewise, when $\beta > \beta_1^*$, all trajectories on the inner shell whirl around the central hole because $\dot{\theta}_2 < 0$ there.

Since the state of a trajectory at a time t depends continuously on its initial state, there are trajectories on the interior of \mathscr{X}^K that stay close to the boundary and whirl around in θ_k many times before converging to \mathbf{p}_+ as $t \to +\infty$ and to \mathbf{p}_- as $t \to -\infty$. In the pictures of \mathscr{D} , whirling in θ_2 takes place close to the inner shell where $x_1 = 0$, or equivalently, $x_2 = 1$. That is, when strategy 2 is very popular, its associated resource is depleted rapidly until it crashes. Sometimes, x_2 decreases enough that the trajectory passes through the θ_2 nullcline and stops whirling. In other



Figure 8. Trajectories that whirl (a) zero, (b) once, (c) twice, and (d) three times around the central hole before converging to \mathbf{p}_+ . All start on the annulus $\theta_2 \cong 0$ and proceed clockwise. Parameters: $\beta = 0.4$, $a = 1, \gamma = \pi/4$.

cases, the resource recovers quickly enough to go through more crash and recovery cycles before x_2 decreases significantly.

When $\beta_1^* < \beta < \beta_K^*$, it appears that most trajectories in the interior of \mathscr{X}^K eventually converge to \mathbf{p}_{\pm} as $t \to \pm \infty$. These trajectories will be called *ordinary*. There must also be a low-dimensional set of *extraordinary* trajectories on the interior of \mathscr{X}^K that do not converge to \mathbf{p}_{\pm} as $t \to \pm \infty$. These ought to exist because there must be separatrices between sets of ordinary trajectories with distinct topological types, that is, those that whirl different numbers of times in the θ_k variables. For example, separatrices form the boundary between ordinary trajectories that converge to \mathbf{p}_+ without further whirling from those that pass close to \mathbf{p}_+ but veer off and whirl around again before finally converging. Potentially, there may also be *hybrid* trajectories that would come in two types. A hybrid trajectory of the first type converges to \mathbf{p}_+ in forward time but not to \mathbf{p}_- in backward time. A hybrid trajectory of the second type converges to \mathbf{p}_- in backward time but not to \mathbf{p}_+ in forward time. It is not yet clear whether any hybrid trajectories exist.

From another perspective, we can consider the dynamics of each resource variable θ_k as taking place on \mathbb{R} . The magnitude of θ_k indicates how many times a trajectory has whirled around the central hole. This unrolls \mathscr{X}^K into a periodic phase space, with a lattice of fixed points that differ by an integer multiple of 2π in each θ_k . The basins of attraction of these fixed points must have separatrices, which can be mapped back into the original \mathscr{X}^K .

The nature of the separatrices is unclear. One possibility is that there are periodic orbits in \mathscr{X}^K of saddle type, and that their stable manifolds form the separatrices. There are also saddle points on $\partial \mathscr{X}^K$ whose stable manifolds are of the appropriate dimension and may form separatrices. However, it is also possible that the separatrices are invariant manifolds with no relatively stable orbits at all. For example, a separatrix might be a tube that nests within itself as it whirls in θ_1 ,



Figure 9. Initial conditions on the annular cross-section of \mathscr{D} where $\theta_2 \cong 0$ that converge to \mathbf{p}_+ (a) directly as in Fig. 8(a); (b) after one whirl in θ_2 as in Fig. 8(b); (c) after two whirls in θ_2 as in Fig. 8(c); (d) after three whirls in θ_2 as in Fig. 8(d). Parameters: $\beta = 0.58 < \beta_K^*$, a = 1, $\gamma = \pi/4$.

within which all orbits rotate irregularly in θ_2 and are all unstable.

It is possible to map out sets of trajectories with particular topological properties numerically. Initially, let us focus on the low-dimensional case of K = 2, and count whirls in θ_2 in forward time only. The resulting pictures show only partial topological information, as whirls in backward time are not counted, and only whirls in θ_2 are considered. As a heuristic, starting from $\theta_2(0) = 0$, if m_2 is the positive integer such that $\theta_2(400)$ and $\theta_2(500)$ both lie between $-2(m_2 + 1)\pi$ and $-2m_2\pi$, then the trajectory is considered to have made m_2 whirls in θ_2 before converging to \mathbf{p}_+ in forward time. The set of initial conditions making a given number of whirls wraps around the phase space in a very complicated way and appears to be fractal, as shown in Figs. 9 and 10.

For smaller values of β , a large subset of \mathscr{X}^2 consists of trajectories that converge to \mathbf{p}_+ in forward time without further whirling. These form the large red region in Fig. 10 (a). For larger values of β , this region is smaller, as shown in Fig. 10 (b).

Looking in both forward and backward time and with general K, the complete topological type



Figure 10. Initial conditions on the annulus $\theta_2 \cong 0$, color coded by how many whirls in θ_2 they make in forward time before going to \mathbf{p}_+ . In (a), $\beta = 0.4$, and in (b), $\beta = 0.58$. Other parameters: a = 1, $\gamma = \pi/4$.



Figure 11. Trajectories of topological type $(m_1, m_2) = (1, 1)$, (1, 2), and (2, 1), using $\beta = 0.58$, a = 1, $\gamma = \pi/4$.

of an ordinary orbit can be expressed as a vector $\mathbf{m} = (m_1, m_2, \dots, m_K)$ of the number of whirls m_k it makes in each θ_k . That is, treating θ_k as a real number,

$$m_{k} = \left\lceil \frac{1}{2\pi} \left(\lim_{t \to +\infty} \theta_{k} - \lim_{t \to -\infty} \theta_{k} \right) \right\rceil.$$
(41)

As was done with the partial topological type in Fig. 8, in the case of K = 2, it is possible to numerically locate example orbits of various complete topological types and display them as shown in Fig. 11.

The sets of orbits of various topological types can also be approximated. They have complicated shapes, are intricately layered, and may not be connected. The numerical procedure is to take points from a cross-section of \mathscr{X}^2 as initial conditions, and integrate forward and backward in time treating each θ_k as a real number. If the estimated values of θ_k at the backward and forward ends are unchanged for a long time interval, the whirl count is calculated from the difference as in Eq. (41). Initial points in that cross section are color coded according to those whirl counts. See



Orbits of type (2, 1)

Figure 12. Cross section $\theta_2 \cong 0$ colored by complete topological type, using $\beta = 0.58$, a = 1, $\gamma = \pi/4$. Bundles of orbits of three topological types $(m_1, m_2) = (1, 1)$, (2, 1) and (1, 2) are shown, with lines to the subset of the cross section from which they were taken. Orbits within each bundle are colored randomly to make the whirling structure visible.

Fig. 12, in which topological types are shown up to four whirls in each of θ_1 and θ_2 . Sets of orbits with higher whirl counts are so finely layered that it is difficult to resolve them visually, so the corresponding initial conditions are left uncolored.

Due to the symmetries of the dynamics, if an orbit of type (m_1, m_2) exists, there should also be an orbit of type (m_2, m_1) . It is not yet clear whether orbits of every possible topological type exist for every choice of parameters.

G. Global consequences of the bifurcation of the interior fixed points at $\beta = \beta_K^*$

The collision and annihilation of \mathbf{p}_+ and \mathbf{p}_- when $\beta = \beta_K^*$ is a local bifurcation, but it has global consequences. Once $\beta > \beta_K^*$, it appears that all trajectories whirl without stopping and there are no longer any stable orbits in \mathscr{X}^K . The result is chaotic oscillations. The well-known horseshoe mechanism^{2,21} appears to be present in the Poincaré section shown in Fig. 13. Chaos appears instantaneously, with no period-doubling cascade. The underlying mechanism is not yet clear; candidates include various crisis-like, explosive, or dangerous bifurcations^{9,23}.

The picture in Fig. 13 is computationally challenging to produce. Starting from the boundary of a strip in the Poincaré section $\theta_2 = 0$, where $0.25 \le x \le 0.75$ and $-0.1 \le \theta_1 \le 0.04$, initial conditions are followed forward in time for one complete whirl, that is, until they return for the first time to the Poincaré section. The first-return point of a trajectory is found by stopping the numerical integration when $\theta_2 = -2\pi \cong 0$. These first-return points are then joined into a polygon. The result is a partial Poincaré or first-return map, showing what happens to each point in the strip when it first returns to the initial annulus. Starting from a coarse set of points on the boundary of the strip, an iterative adaptive refinement procedure produces the final picture. If two adjacent initial conditions result in future points separated by more than 0.01 in Euclidean distance, another initial condition is inserted at the midpoint of the first two and followed forward. This process is repeated until all adjacent initial conditions lead to future points within 0.01, thereby forming a smooth approximation of the boundary of the swoosh in Fig. 13. The choice of $\beta = 0.7$ for this picture was for computational convenience. The calculations as implemented overwhelmed the author's workstation if β was too close to β_K^* . If necessary, that problem could be remedied by writing a more sophisticated program.

The color coding shows which part of the strip maps to which part of the swoosh. The mapping preserves the overall orientation of the strip. The strip stretches in the x_1 direction and squeezes in the θ_1 direction, while folding twice. The Poincaré map appears to have at least three fixed points, one in the red area to the left, one in the green area in the middle, and one in the orange area to the right. Assuming the horseshoes are as the numerical approximation suggest, there are infinitely many more fixed points just in this strip. These correspond to unstable closed orbits in the overall dynamics. Such closed orbits may be assigned a topological type depending on how many whirls they make in each θ_k , similar to the types assigned to ordinary orbits before the bifurcation. It is not yet clear whether orbits of all possible types exist.



Figure 13. Poincaré (first-return) map indicating horseshoes. Initial conditions are taken from the edges of a strip in the annulus $\theta_2 = 0$. Each is mapped forward in time until $\theta_2 = -2\pi$, resulting in the swoosh. Parameters: $\beta = 0.7$, a = 1, $\gamma = \pi/4$.



Figure 14. Part of a trajectory in the chaotic regime. Parameters: $\beta = 0.7$, a = 1, $\gamma = \pi/4$, $\theta_1(0) = 0$, $\theta_2(0) = 0$, $x_1(0) = 0.6$. Top: Trajectory in 3D. Bottom left: x_1 component as a function of time. Bottom right: $\cos \theta_1$ component as a function of time.

The origin of chaos here seems to be that ordinary orbits of many topological types are present before the bifurcation at $\beta = \beta_K^*$. These fill the bulk of the phase space. Unstable extraordinary orbits form the separatrixes between sets of ordinary orbits of different types. Once \mathbf{p}_+ and $\mathbf{p}_$ collide and vanish, ordinary orbits can no longer exist. Remnants of the separatrix structure may persist, but there are no longer any stable orbits.

Note that the θ_k 's are still coupled in this regime through their dependence on the x_k 's. The chaotic behavior is not simply a collection of independent, unsynchronized, nonlinear oscillators. A sample trajectory with K = 2 is shown in Fig. 14. Note that x_1 varies from nearly 0 to nearly 1, and θ_1 whirls irregularly with significant backtracking. Thus, all three variables are non-trivially coupled.

As was noted in Section II E 2, for larger *K*, portions of $\partial \mathscr{X}^K$ may be interpreted as *L*-strategy replicator dynamics of the same form, with the other K - L population variables x_j fixed at zero and the corresponding resource variables θ_j decoupled. When β passes through β_L^* , the same kind of transition to chaos happens within those components of the boundary, so lower-dimensional chaos appears there as β increases.

H. Periodic orbit imposed by symmetry

As a consequence of the permutation symmetry of Eqs. (10) to (11), one periodic orbit of topological type (1, 1, ...) is present for sufficiently large β . It is given by

$$x_k(t) = \frac{1}{K} \text{ for all } k \tag{42}$$

and each θ_k is a solution of the initial value problem

$$\dot{\theta}_{k} = a \times \left(\cos\left(\theta_{k} + \gamma\right) - \cos\gamma - \frac{\beta}{K} \right)$$

$$\theta_{k}(0) \cong 0$$
(43)

Any initial value used for all θ_k produces the same orbit with different time parameterization. See Fig. 15.

For $\beta < \beta_K^*$, this periodic orbit does not exist, because initial conditions of the appropriate form generate ordinary trajectories that converge to \mathbf{p}_{\pm} instead of tracing a closed curve. It can exist for $\beta > \beta_K^*$ because $\dot{\theta}_k$ in Eq. (43) is always strictly negative. In Fig. 13, it corresponds to the fixed point of the Poincaré map indicated by the green area in the middle of the strip and swoosh.



Figure 15. Periodic orbit as in Eqs. (42) to (43). Parameters: a = 1, $\gamma = -\pi/4$, $\beta = 0.7$.

Further numerical evidence confirms that this orbit is of saddle type, consistent with its position in the horseshoe. See Fig. 16 for part of a Poincaré section through the annulus given by $\theta_2 \approx 0$. The axes are x_1 and θ_1 . The periodic orbit passes through the center of the picture at $x_1 = 1/2$ and $\theta_1 \approx 0$. The blue circle is of radius 0.01, and orbits initialized on it return to the Poincaré section to form the orange ellipse. The Poincaré map clearly stretches its phase space in one direction while squeezing in another, implying that the central fixed point is a saddle.

It is possible that the stable and unstable manifolds of this closed orbit intersect and form a homoclinic tangle, which would provide another explanation for the overall chaotic behavior¹⁰.

III. CONCLUSION

The standard replicator equation was modified so that the payoff from playing a strategy is a function of the state of a corresponding renewable resource. New variables were included representing the states of the resources, and their dynamics include terms so that each is depleted in proportion to the fraction of the population using the associated strategy. Under some conditions, the behavior of trajectories is relatively simple. However, many open questions remain.

When the depletion rate parameter β is low, most initial conditions with a non-zero fraction of the population using each strategy converge in forward time to a fixed point \mathbf{p}_+ that represents a state in which all strategies are equally popular and all resources are at stable levels, depleted



Figure 16. Detail of the Poincaré map in the vicinity of the periodic orbit. The overall cross section is the annulus $\theta_2 \cong 0$. The left picture (a) shows the circle of initial conditions and the ellipse of return points. The right picture (b) overlays lines connecting sample initial points to their return points, to indicate the inherent shear. Parameters: a = 1, $\gamma = -\pi/4$, $\beta = 0.7$.

at a sustainable rate. Initial conditions in which some strategies are absent have similar behavior, restricted to the subset of the phase space in which those strategies are permanently extinct. Resources do not crash, and geometrically, it is not possible for trajectories to whirl around the phase space.

When the depletion rate increases through $\beta = \beta_1^*$, it becomes possible for resources to crash and trajectories to whirl. A whirl in θ_k corresponds to exhaustion of the resource, followed by recovery. While $\beta < \beta_K^*$, most trajectories seem to undergo finitely many whirls in each θ_k between converging in forward time to \mathbf{p}_+ and in backward time to \mathbf{p}_- . It is unknown whether orbits with every possible topological type of whirling exist.

As the depletion rate increases further, through $\beta = \beta_K^*$, all resources are depleted so rapidly that they are trapped in an irregular crash-and-recovery cycle. Numerical evidence points to the immediate appearance of chaos at this value of β , without a period-doubling cascade. It seems to be a consequence of the existence of a complicated family of invariant manifolds that form the separatrices between sets of ordinary orbits of different topological types for $\beta < \beta_K^*$. These may be stable manifolds of unstable periodic orbits, or they may be something else entirely. It is not yet known exactly which aspects of this separatrix structure persist and in what sense as β increases.

The approach taken in this article to the general problem of replicator dynamics with depletable resources was to work in an arbitrary number of dimensions, but with highly symmetric dynam-

ics. Every strategy is exactly equivalent to every other strategy. Consequently, the bifurcation in which \mathbf{p}_+ and \mathbf{p}_- collide is degenerate. An alternative approach would be to work in only a few dimensions and break some of the symmetry, thereby unfolding this degenerate bifurcation and perhaps allowing for other behavior, such as stable oscillations.

Another possible extension is to include both a general two-player game and resource dynamics. Fitness would be the sum of the game payoff as in Eq. (4) and the resource term $\cos \theta_k$ introduced in Section IB,

$$c_k = \cos \theta_k + \sum_j A_{k,j} x_j. \tag{44}$$

Again, this breaks the symmetries of Eqs. (10) to (11), so it would be necessary to begin with low-dimensional cases.

Another possible extension is to allow strategies to deplete multiple resources at different rates. It requires a consumption matrix **B** such that $B_{k,j}$ is the equivalent of β for how quickly strategy *j* consumes resource *k*. The resource dynamics Eq. (11) would then change to

$$\dot{\theta}_{k} = a \times \left(\cos\left(\theta_{k} + \gamma\right) - \cos\gamma - \sum_{j} B_{k,j} x_{j} \right).$$
(45)

It is also possible to combine Eq. (44) and Eq. (45), although there would be so many parameters that a complete bifurcation analysis may not be feasible.

SUPPLEMENTARY MATERIAL

Mathematica notebooks used to create the pictures in this article are posted as supplementary files.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available within the article and its supplementary material.

AUTHOR DECLARATIONS

The author has no conflict of interest to disclose.

REFERENCES

- ¹Peter Ashcroft, Philipp M. Altrock, and Tobias Galla. Fixation in finite populations evolving in fluctuating environments. *Journal of The Royal Society Interface*, 11(100):20140663, November 2014.
- ²Robert L. Devaney. *An Introduction to Chaotic Dynamical Systems*. Studies in Nonlinearity. Westview Press, Boulder, Colo, 2nd ed., paperback ed edition, 2003.
- ³Punithan Dharani and RI (Bob) McKay. Evolutionary dynamics and ecosystems feedback in two dimensional daisyworld. In *Artificial Life 13*, pages 91–98. MIT Press, July 2012.
- ⁴Richard Durrett. *Stochastic Calculus: A Practical Introduction*. Probability and Stochastics Series. CRC Press, Boca Raton, 1996.
- ⁵Bard Ermentrout. Ermentrout-Kopell canonical model. *Scholarpedia*, 3(3):1398, March 2008.
- ⁶Bard Ermentrout and David H. Terman. *Mathematical Foundations of Neuroscience*. Number 35 in Interdisciplinary Applied Mathematics. Springer, New York, NY, 2010.
- ⁷G. B. Ermentrout and N. Kopell. Parabolic bursting in an excitable system coupled with a slow oscillation. *SIAM Journal on Applied Mathematics*, 46(2):233–253, April 1986.
- ⁸Shiping Gao and Jinling Liang. The effects of resource limitation and consensual incentives on cooperation. *Physics Letters A*, 384(35):126904, December 2020.
- ⁹Celso Grebogi, Edward Ott, and James A. Yorke. Crises, sudden changes in chaotic attractors, and transient chaos. *Physica D: Nonlinear Phenomena*, 7(1):181–200, May 1983.
- ¹⁰Kevin Hockett and Philip Holmes. Josephson's junction, annulus maps, Birkhoff attractors, horseshoes and rotation sets. *Ergodic Theory and Dynamical Systems*, 6(2):205–239, June 1986.
- ¹¹J. Hofbauer and K. Sigmund. *Evolutionary Games and Population Dynamics*. Cambridge University Press, 1998.
- ¹²Weini Huang, Bernhard Haubold, Christoph Hauert, and Arne Traulsen. Emergence of stable polymorphisms driven by evolutionary games between mutants. *Nature Communications*, 3(1):919, June 2012.
- ¹³W. Garrett Mitchener. Bifurcation analysis of the fully symmetric language dynamical equation.
 Journal of Mathematical Biology, 46(3):265–285, March 2003.
- ¹⁴W. Garrett Mitchener. Game dynamics with learning and evolution of universal grammar. Bulletin of Mathematical Biology, 69(3):1093–1118, January 2007.

- ¹⁵W. Garrett Mitchener and Martin A. Nowak. Competitive exclusion and coexistence of universal grammars. *Bulletin of Mathematical Biology*, 65(1):67–93, January 2003.
- ¹⁶W. Garrett Mitchener and Martin A. Nowak. Chaos and language. *Proceedings of the Royal Society of London B: Biological Sciences*, 271(1540):701–704, April 2004.
- ¹⁷Archan Mukhopadhyay, Suman Chakraborty, and Sagar Chakraborty. Chaos and coexisting attractors in replicator-mutator maps. *Journal of Physics: Complexity*, 2(3):035005, May 2021.
- ¹⁸Martin A. Nowak. *Evolutionary Dynamics: Exploring the Equations of Life*. Harvard University Press, Cambridge, MA, 2006.
- ¹⁹Martin A. Nowak and Karl Sigmund. Evolutionary dynamics of biological games. *Science*, 303(5659):793–800, February 2004.
- ²⁰Peter Schuster and Karl Sigmund. Replicator dynamics. *Journal of Theoretical Biology*, 100(3):533–538, February 1983.
- ²¹S. Smale. Differentiable dynamical systems. *Bulletin of the American Mathematical Society*, 73(6):747–817, 1967.
- ²²Peter D. Taylor and Leo B. Jonker. Evolutionary stable strategies and game dynamics. *Mathe-matical Biosciences*, 40(1-2):145–156, July 1978.
- ²³J. M. T. Thompson, H. B. Stewart, and Y. Ueda. Safe, explosive, and dangerous bifurcations in dissipative dynamical systems. *Physical Review E*, 49(2):1019–1027, February 1994.
- ²⁴Vandana Revathi Venkateswaran and Chaitanya S. Gokhale. Evolutionary dynamics of complex multiple games. *Proceedings of the Royal Society B: Biological Sciences*, 286(1905):20190900, June 2019.